

Relationship between structure and function of mammalian vibrissa

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Abstract The structure of mammalian vibrissa was observed microscopically and the relationship of morphology and function was discussed. The vibrissa is conical. The elasticity and tenacity of vibrissa are stronger than that of pelage hair. The scales are shaped irregular on vibrissa shaft except for the root part, because of fractional damages. This type of scales is of great importance in preventing the vibrissa from being totally destroyed. Cortex of vibrissa is observed very well developed, thus its elasticity and tenacity work well in touching and sensing. Medulla of vibrissa is not well developed because vibrissa has been evaluated to fail in warm-keeping function.

Key words: Mammalian vibrissa, Elasticity, Tenacity, Pelage hair

Materials and methods

Materials

The vibrissae in this experiment were sampled from Harbin Zoo and the Specimen Room of Northeast Forestry University. These samples cover 4 families, Carnivora, Perissodactyla, Rodentia and Primats.

Methods

The whole vibrissa with hair root was sampled in various sites of mammal body such as mouth, eyelid, face, neck and jaw. By comparison, the author did not find significant differences in vibrissa structure of different parts of body. So the vibrissa of cheek is used for observation and comparison.

Samples were observed with light microscope and SEM. Hair scales and medullas were observed through OLYMPUS light microscope and KYKY-1 000B scanning-electron microscope. Hair length, diameter and medulla diameter were measured under light microscope. The data were treated by statistical methods.

Results and discussion

Morphological structure of mammalian vibrissa

The vibrissa is longer than the pelage hair. The volume of vibrissa follicle is 5 ~ 6 times larger than that of the pelage hair. The vibrissa is connected with arrector muscle and is nourished by sinus, which is full of blood vessels. The result of observation shows that the characteristics like diameter, hardness, elasticity

color and length are significantly different in vibrissae from different species (Table 1). Even in the same species, vibrissae from different part exhibit polymorphic characters. Based on diameter, hardness, elasticity and length, the matured vibrissa can be divided into four types, namely type A, B, C and D.

Type A: The root diameter is more than 300 μm , with the strongest hardness and elasticity.

Type B: The root diameter is between 200 μm and 300 μm , the hardness and elasticity inferior to type A.

Type C: The root diameter is between 120 μm and 200 μm , hardness and elasticity weaker than type B.

Type D: The root diameter is less than 120 μm , with the weakest hardness and elasticity.

Almost all mammals have vibrissa in the sit of cheek except for a few species such as Phayre's leaf-monkey. The vibrissa in the cheek has stronger elasticity and hardness belonging type A and B. Canidae and Felidae vibrissae are mainly of type A. Mustelidae, Viverridae, Rodentia and Primates vibrissae are mostly of type B. Mills F. proved that cheek vibrissa protected animal's face from being destroyed. Almost all mammals have vibrissa in the corner of eyelid, which is mainly of type B and type C. They can protect eyes and play a supplementary role in their eyesight. It was considered that a hunting dog could judge the wind direction by vibrissa and then turned back to detect the smell from the targets. Mammalian vibrissa was simple, mainly pigmented black and white, seldom yellow and brown. It varies in length. The facial vibrissa is well developed in tree living species, aquatic and semi-aquatic species, but not so developed in herbivore, especially in cattle and deer.

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The development degree of vibrissa was related to the very life style of the species (Fig. 1.)

Table 1. The morphological comparison of mammalian vibrissa

Family	Species	Sample site	Type	Color	Length/cm	Quantity
Canidae	<i>Vulpes ferrilata</i>	Cheek	B	Black	4.0~7.0	7
		Beside mouth	C	White	3.0~6.5	12
		Lower jaw	C	White	2.0~4.0	2
			A	Black	3.0~7.0	3
		Lower neck	B	Black	1.0~3.0	5
	<i>Vulpes vulpes</i>	Cheek	A	Black	6.0~8.0	3
			-	Black	4.0~5.0	3
		Beside mouth	C	White	0.7~1.0	8
		Lower jaw	B	Black	5.0~7.0	5
		Lower neck	B	Black	5.0~7.0	3
Felidae	<i>Felis lynx</i>	Cheek	A	White	6.0~7.0	4
		Beside mouth	C	White	3.0~3.5	4
		Upper eyelid	C	White	4.0~6.0	3
	<i>Felis chaus</i>	Cheek	B	White	3.0~4.0	5
			C	White	1.0~2.0	6
		Upper eyelid	C	Yellow	4.0	1
			C	White	1.0~3.0	4
	<i>Profelis temminckia</i>	Cheek	A	Black	5.0~6.0	4
			B	Black	5.0~6.0	6
			C	Black	1.0~3.0	10
		Face	B	Black	4.0~5.0	2
			C	Black	5.0~6.0	2
	<i>Felis bengalensis</i>	Upper eyelid	B	Black	3.0~4.0	5
		Cheek	A	Black	6.0~7.0	6
		Upper eyelid	B	Black	3.0~4.0	5
	<i>Felis manul</i>	The same level of nostril	B	Black	3.0~4.0	2
		Cheek	C	White	5.0~6.0	1
		Upper eyelid	C	White	4.0~5.0	14
Pvocyonidae	<i>Ailurus fulgens</i>	Cheek	B	White	5.0~7.0	10
			C	White	3.0~5.0	6
		Face	B	White	4.0~7.0	2
		Upper eyelid	C	White	1.5~5.0	3
		Cheek	B	White	7.0	1
	<i>Herpestes javanicus</i>		C	White	4.0~6.0	14
		Face	B	White	6.0~7.0	1
		Upper eyelid	C	Black	4.0~5.0	3
		Cheek	C	Black	1.0~2.0	2
			C	White	2.0	2
	<i>Paguma larvata</i>	Cheek	D	Yellow	0.1~1.0	9
		Cheek	B	Black	6.0~7.0	5
			C	White	4.0~5.0	4
	<i>Viverra megaspila</i>	Cheek	B	Black	5.0~7.0	4
		Face	C	Black	1.5~7.0	2
		Upper eyelid	B	Black	3.5~4.0	4
Mustelidae	<i>Prionodon pardicolor</i>	Cheek	B	Black	3.0~4.0	1
			C	White	2.0~3.0	10
		Face	C	Yellow	6.0~7.0	2
		Upper eyelid	B	Black	2.0~2.5	4
		Cheek	B	Yellow	3.0~4.0	4
	<i>Mustela altaica</i>	Upper eyelid	D	Yellow	4.0~5.0	3
		Cheek	B	Yellow	4.0~5.0	4
		Upper eyelid	D	White	4.0~5.0	10
	<i>Mustela erminea</i>	Cheek	D	White	4.0~5.0	4
		Cheek	B	Black	5.0~6.0	4
			C	Black	4.0~5.0	7
	<i>Martes foina</i>	Upper eyelid	C	Black	3.0~6.0	6
		Cheek	B	Black	4.0~5.0	10
		Face	B	Black	2.0~4.0	3
		Upper eyelid	C	Black	2.0~5.0	4

Continued Table 1

Family	Species	Sample site	Type	Color	Length/ cm	Quantity
<i>Mustela eversmann</i>	Cheek	B	Black	5.0	5	
		C	Black	4.0~5.0	4	
		B	Black	4.0	1	
	Face	C	Black	3.0	1	
		B	Black	1.0~2.0	3	
	Upper eyelid	C	Black	2.0	1	
<i>Lutra lutra</i>		B	Black	1.0~2.0	3	
Cheek	A	Black	3.0~5.0	3		
	A	White	2.0~4.0	8		
Upper eyelid	C	Yellow	3.0	1		
	B	Black	3.0	2		
<i>Martes flavigula</i>	Cheek	A	Black	2.0~3.0	2	
			Black	1.0~2.0	7	
	Upper eyelid	C	Black	2.0~3.0	3	
		B	Black	3.0	1	
	<i>Presbytis phayrei</i>	Beside lip	C	White	0.5~1.0	
		Eyelash				
<i>Rhinopithecus roxellanae</i>	Cheek	C	Black	1.0		
	Beside lip	C	Black	2.0~3.0		
Cricetidae	<i>Ondatra zibethicus</i>	Cheek	C	Black	2.0~3.5	6
			B	Black	3.5~4.0	6

The microstructure of mammalian vibrissa

The vibrissa is analogous to the pelage hairs which consist of three layers, scale, cortex and medulla.

The scale and cortex of vibrissa are better developed than that of pelage hairs, but the medulla is less developed. In some species such as slow lorises in Primates have no medulla in vibrissa.

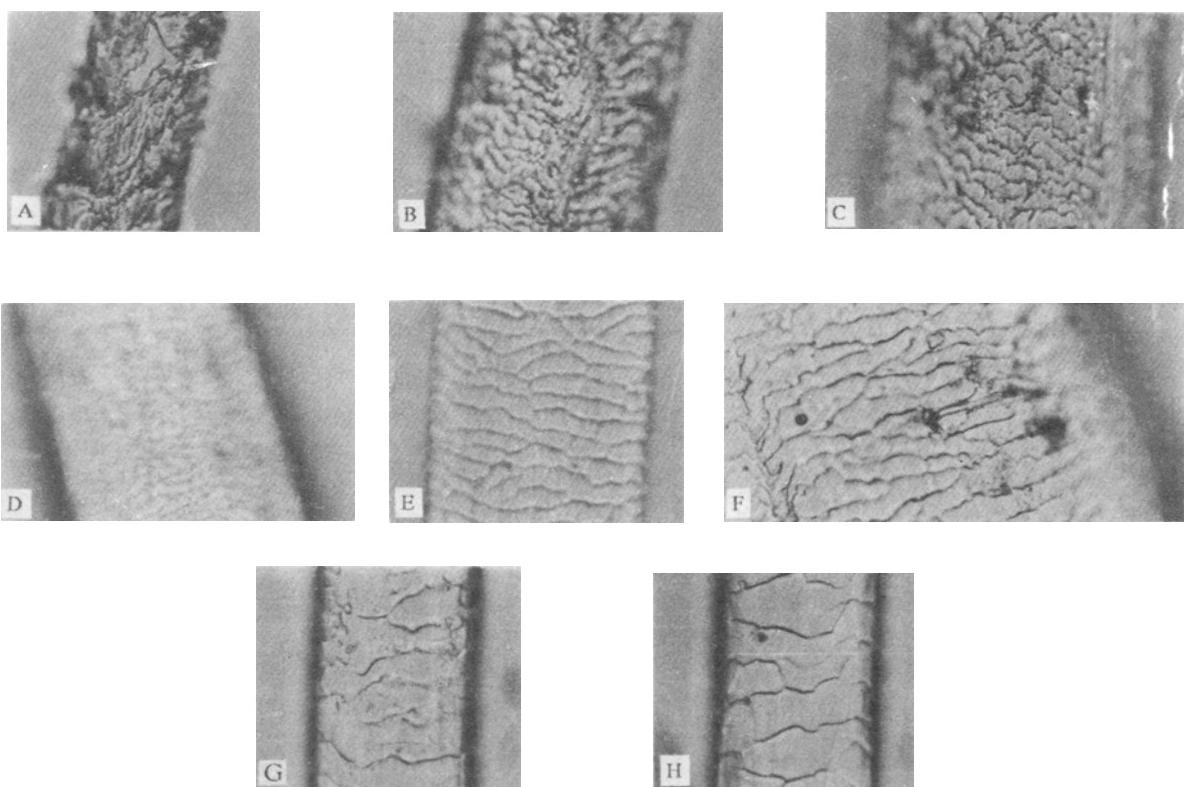


Fig. 1. Microscopic graphs of vibrissae scales

A. Vibrissa tip of Mink (*Mustela vison*); B. Siberian weasel (*Mustela sibirica*); C. Musk rat (*Ondatra zibethicus*); D. Vibrissa mid-part of Mink (*Mustela vison*); E. Musk rat (*Ondatra zibethicus*); F. Frost fox; G. Vibrissa root of Musk rat (*Ondatra zibethicus*); H. Golden monkey (*Pygathrix roxellanae*).

According to the scale pattern, taking red fox in *Canidae* as examples, analyzing the character of scales under light microscope, the spaceman of red fox vibrissa shows that the scales on the top of vibrissa have been terribly spoiled, some are even totally removed. Scales are shaped to be regular smooth on the basis of newborn vibrissa. It was reported that scales of irregular wave type came from the spoil of smooth type scales. Scales on the top of guard hair had irregular waves, which were caused by friction (Fig.1. A~C). In animal daily life, vibrissa is very possibly touching other objects. So friction often exists to destroy scales. Toward the root of hair, regular smooth type scales can be observed and they are arranged evenly. The distance between scale edges is around $23\mu\text{m}$. The part of scale looks like transitional type from irregular wave to regular smooth (Fig.1. D~E). Approaching root of hair, scales become smoother, the edge distance differs slightly. From top to root, the sequence of vibrissa type is irregular wave type, transitional type and regular smooth type (Fig.1. F~H and Table 2). According to Table 2, irregular wave type occupies the most part of the vibrissa shaft, more than 80%. The distance of vibrissa scales exceeds $25.45\mu\text{m}$. By contrast, the distance of scale edges of pelage hair is more than $25.45\mu\text{m}$. The proportion of regular smooth type is approximately equal to that of transitional type. There

is obvious difference between the scale type of vibrissa and pelage hair. There are many kinds of scale types in pelage hair, such as disorganized petal type, sharp petal type, egg petal type and irregular smooth type. The distance between scale edges is also large. In function vibrissae differ from pelage hairs.

As far as function is concerned, the delicate distribution of vibrissa scales coincides with its protection. The inseparable connection among scales forms a steady wall, which can keep vibrissa apart from the outer world, so that the internal structures can remain stable.

The reason that there are no other scale pattern except regular smooth and irregular wave can be that: the growth of vibrissa is so rapid that scales overlap and transform are very thin multilayers.

Vibrissa cortex layer of most mammalian species is well developed, although cortex is shaped differently in different species (Fig. 2). The cortex layer was very hard because keratins contained. The thickness of cortex determines its tensile strength. It is much thicker than that of pelage hairs, which illustrates that vibrissa's tensile strength is by far stronger. These are the reasons that vibrissa can give assistance but not be broken when the mammals search food, attack preys and protect themselves.

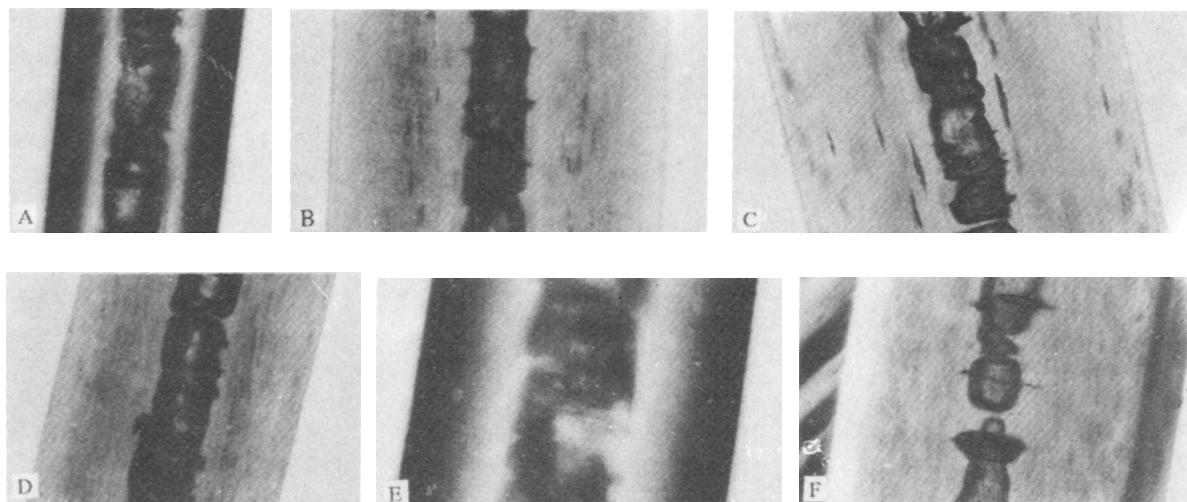


Fig. 2. Microscopic structure of vibrissae medulla

A. Frost fox; B. Roe deer (*Copreolus capreolus*); C. Red fox (*Vulpes vulpes*); D. Siberian weasel (*Mustela sibirica*); E. Raccoon-dog (*Nyctereutes procyonoides*); F. Golden monkey (*Pygatryrix roxellanae*).

The medulla layer isn't well developed in vibrissa (often less than 30%) (Fig. 2). Most of them are uncontinuous and shaped column. Commonly, the better developed the medulla is, the less tenacity the hair is. Thus vibrissa tenacity is much stronger than that of

pelage hairs. Moreover, vibrissae don't have warm-keeping function. From the view of evolution, it is reasonable that the vibrissa loses medulla in which air is kept for warm keeping (Fig. 2).

nutritional significance. Proanthocyanidins also differ in the position (C_4 to C_8 vs. C_4 to C_6) and stereochemistry of their interflavan bonds. They are generally assumed to be linear polymers, they are the evidence of branching. Virtually all flavanol units of proanthocyanidins are hydroxylated at positions 5 and 7 on their ring A, but they differ in the degree of hydroxylation of their ring B; the catechol pattern of cyanidin is most common.

Hydrolyzable tannins

Hydrolyzable tannins (tannin acids), are composed of gallic acid. Additional depsidically linked galloy groups are usually present. The distinction between condensed and hydrolyzable tannins is somewhat blurred by the occurrence, especially in tea, of hybrid molecules containing both galloy groups and flavan-3-ol units. The gallic-acid-containing tannins are alkali labile and are hydrolyzed by astrointestinal esterases or by tanning acyl hydrolase, which is secreted by certain fungi, yeast, and bacteria.

Assay

The amount of tannin depends on the developmental stage of the plant and the environmental conditions under which it grows. Because tannins are secondary products, and are not involved in energy-producing metabolic reactions or reproductive processes. There is no minimum requirement for tannins in plants, and the amount of tannins present varies widely among plant species, crop cultivating of the same species, and various tissues of the same plant. In the process of domestication of crop and food plants from progenitors that contained tannins, the amount of tannins in the plant tissues must have been diminished by selection for improved palatability. In contrast, herbivore of undomesticated plants must result in selection for high effective levels of tannins if these metabolites do deter herbivore. The amount of tannins present in food and forage crops is therefore generally lower than the amount in undomesticated plants. However, many relevant researches have been done on crop plants such as legumes, tea, and sorghum because of their economic importance. Both condensed and hydrolyzable tannins interact with proteins to form soluble or insoluble complexes. Under mild conditions, the interaction is based on noncovalent, hydrogen and hydrophobic bonds. The complexes formed can be dissociated by detergents, which disrupted hydrophobic interactions, or by high pH, which ionized the phenolic hydroxyl and thus destroyed its hydrogen-bonding ability. These two kinds of tannins are susceptible to oxidation at high pH. The oxidation products can form covalent bond with nucleophiles

including the amino or sulfhydryl groups of proteins.

The methods of determining the tannins are based on two ways: chemical assay and protein-binding assay. Chemical assay is useful for determining the amount of tannin in a sample and for elucidating the structure of the tannin. Protein-binding assay is more useful for determining the potential biological activity of tannin in a sample. The analyst must decide whether a commercial or a noncommercial tannin standard is appropriate.

Tannins as antifeedants for herbivores

From the biological point of view, the importance of tannins lies in their effectiveness of antifeedants, the relevant property is "astringency", rendering the tissue unpalatable by precipitating salivary protein or by immobilizing enzymes, impeding the invasion of the tissue of the host by the parasites. Due to astringent tannins, these lead to reduction in the voluntary feed intaking. Reports of grazing tests showed that animals consumed more plants of the low tannin than those of high tannin. Tannins also diminish the permeability of the gut wall, by reacting with the outer cellular layer of the gut, so the passage of the nutrients through the gut wall is reduced. Tannins in feed diminish the digestibility of the dry matter and of the nitrogen, this can be explained on the basis of the inhibition of digestive enzymes. Tannin is a potent inhibitor of digestive enzymes due to their capacity to bind with enzyme proteins as well as the substrate. The tannins can affect the enzymes by two aspects:

1. Reducing the solubility of the enzyme protein by forming insoluble protein-phenolic complexes.
2. Inhibiting the enzyme activity by forming a soluble but inactive enzyme-inhibitor complex.

Therefore, competitive and noncompetitive reaction kinetics can be visualized for the inhibition of enzymes by tannins.

The apparent contributions of tannins to plant defense may give rise to unwarranted assumptions that defense is the "purpose" of tannin biosynthesis.

However, Haslam, E. (1979) showed that condensed tannins are metabolic byproducts of the biosynthesis of the parent flavan-3-ols. The hydrolyzable tannins have not been selected for their capacity to bind protein, Haslam, E. has also speculated that tannins may be the "loot in the garbage bin of plant metabolism". In the point of view of efficiency of energy utilization, the concept of tannins as useless waste byproducts is difficult to accept. Not only considerable energy required to synthesize tannins is, but also the preservation and transmission of the genetic information required for production of their biosynthetic enzymes is unlikely unless these enzymes or their tannin products have significantly benefited the plants

that produced them.

Tannins do play a role in plant defense against herbivore. 38 independent feeding tests on the effect of dietary tannins concluded that "animals tend to reject astringent food was not doubt, but what they avoided by doing so was still something of an open question". In order to defend herbivore, tannins must induce a negative response when consumed, presumably because of an immediate unpleasant sensation, antinutrition and toxic effects.

Physiological mechanisms for defending against dietary tannins include diminishing the tannin availability by formation of an inert complex with endogenous proteins, prevention of protein precipitation by formation of a complex with surfactants. The other defending physiological mechanisms are modification of gut environment to higher pH to minimize interaction of similarly negatively charged tannins and proteins, degradation or modification of condensed tannins in the gut or diminishment of intake by lowing the basal metabolic rate. Perhaps the best characteristics of these mechanisms are the tannin binding. Proline-rich salivary proteins induced in rats and mice by tannin consumption. These salivary proteins are produced constitutively in many other herbivores including humans, domestic and wild mammals. Without physiological defenses, consumption of tannins would have much more serious consequence for herbivores.

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